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### DIRECT AND INDIRECT EFFECTS OF PEREGRINE FALCON PREDATION ON SEABIRD ABUNDANCE

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**ABSTRACT.**—Peregrine Falcons (*Falco peregrinus*) have become conspicuous members of the bird assemblage at Tatoosh Island, Washington, since 1983. We have sufficient before and after observations and data to conclude that two species of storm-petrel (*Oceanodroma* spp.) show no significant population trends (as based on catch per hour in standardized mist nets from 1978–1988) and that numbers of both Cassin's (*Ptychoramphus aleuticus*) and Rhinoceros (*Cerorhinca monocerata*) auklets, the primary falcon prey, are probably declining. An important effect of falcons is their consumption of Northwestern Crows (*Corvus caurinus*) or simply restriction of crow activities. The numbers of Common Murres (*Uria aalge*) and Pelagic Cormorants (*Phalacrocorax pelagicus*) that inhabit Tatoosh have increased markedly, probably due to significantly decreased crow-related egg predation. The fledging rate of Black Oystercatchers (*Haematopus bachmani*) approximately doubled in 1987, when one falcon routinely ate crows. These relationships appear to be independent of the locally abundant Glaucous-winged Gulls (*Larus glaucescens*). We conclude that the indirect, positive effects are at least as important to seabird abundance patterns as are direct, negative effects. We suggest that more attention be paid to corvid activities near seabird colonies and, especially, that the impact on populations of small alcids or other prey be considered when planning conservation efforts to augment the population of an effective avian predator. Received 9 January 1989, accepted 13 September 1989.

MOST analyses of multispecies assemblages of birds have focused on some aspects of habitat structure, intraguild dynamics, or factors that promote resource use and coexistence (MacArthur 1958, Root 1967, Cody 1974, Wiens and Rotenberry 1980, Holmes and Recher 1986). Such approaches are often constrained by moral and legal considerations which prevent experimental modification of, or direct intervention in, the study system. The interpretation of different factors usually relies on correlative evidence. We agree with the necessity for some constraints, but we believe that if bird assemblages were subject to direct experimentation as are, for instance, some insect (Root 1973, Kareiva 1987) or rocky intertidal communities (Paine 1966, Dayton 1971), a clearer measure of the focus, intensity, and consequences of inter-

action would be obtained. Fortunately, some insight can be gained by following events subsequent to a human or environmental perturbation of the system. For example, Moulton and Pimm (1983) noted the shifting species composition of Hawaiian exotics associated with new introductions. Wootton (1987) has suggested competitively induced repression of other passerines after House Finch (*Carpodacus mexicanus*) invasion. Boersma (1978), Schreiber and Schreiber (1984), and Hodder and Graybill (1985) examined the influence of El Niño events on reproduction and survival of seabirds.

Another kind of ecologically potent environmental force is the reestablishment of a major carnivore. In Washington state, the Peregrine Falcon (*Falco peregrinus*) historically was a "common permanent resident coastwise" and "a fair-

ly common species on the off-shore islets from Flattery Rocks to Cape Disappointment" (Jewett et al. 1953: 186). We assume that its local numbers were reduced, as they were worldwide, by extensive use of organochlorine-based pesticides and the falcons' sensitivity to them (Ratcliffe 1980). Their increasingly successful reintroduction (Cade et al. 1988) throughout most of North America provides an unusual opportunity to study the influence of bird predation on avian community structure. This circumstance has much to recommend it. The Peregrine Falcon is native, not exotic, and the interactions between species are thus apt to be "natural." A single forcing factor is involved; and peregrines prey almost exclusively on birds (Fisher 1893). As in other avian community studies in which predators were considered and prey dynamics tracked for >1 yr (for instance, Furness 1981, Petersen 1982), substantial changes are evident. These include indirect effects, as the experimental study of Slagsvold (1980) has demonstrated. Such patterns are well documented in other communities (e.g. Carpenter and Kitchell 1988). We report on the population responses of a mixed seabird assemblage to the increased local abundance of Peregrine Falcons.

#### STUDY AREA AND METHODS

All our observations were made at Tatoosh Island, Washington (48°24'N, 124°44'W). The island is actually a collection of interconnected islets with a combined surface area of ca. 6 ha. Vegetation is primarily salal (*Gaultheria shallon*) and salmonberry (*Rubus spectabilis*), with 15–20 emergent but wind-pruned sitka spruce (*Picea sitchensis*). There are not now, and apparently never have been, any resident land mammals. The island was a traditional fishing and egg site for the Makah Indians, was occupied by the U.S. Coast Guard or its antecedents from ca. 1850–1976, and currently is uninhabited, although the navigational aids are maintained and our research programs require frequent visits. A further description accompanied by an aerial photograph can be found in Paine and Levin (1981). The island is an important seabird breeding site (Table 1). Two species of cormorants, two of storm-petrels, five alcids, the highest breeding density of Black Oystercatchers (*Haematopus bachmani*) in Washington state, and one gull use the island.

The data supporting our conclusions have been gathered since 1968. Before 1987, however, they were independent of any conception of how falcons might influence multispecies avian assemblages. Since 1972, the island was visited by at least one of us 7–16 times

per year. Each trip lasted an average of ca. 4 days. In general, 50–70 days each year encompassing all seasons have been spent on Tatoosh. Details of how we estimated population trends are discussed individually because the techniques varied greatly from species to species.

#### POPULATION TRENDS

*Peregrine Falcon*.—Paine has recorded falcon sightings since the U.S. Coast Guard facility was automated in November 1976. In general, the proportion of trips each year on which one or more falcons were observed (Fig. 1) has increased steadily. These data as given are highly conservative because most Tatoosh trips last 4–6 days and even a single sighting constitutes a positive record for the interval. Since 1983, falcons have been seen almost every day and commonly hunt around Tatoosh. A maximum of 5 individuals was seen simultaneously. Before 1977 sightings were rarer. Field notes covering the interval of 1956–1980 and generously supplied by visiting ornithologists (F. R. Richardson, 28–29 July 1956, 15–17 July 1959; D. R. Paulson, 6–8 June 1970; M. Perrone, 9–10 June 1971; D. Wood, 9–15 July 1974, 21–24 July 1975; and G. B. Van Vliet, 27–30 June 1980) recorded no Peregrine sightings. If data were available to measure the intensity or frequency of falcon activities, a rise initiated ca. 1980/1981 would be indicated. It is not possible to distinguish the relative contribution of migrants and a pair breeding ca. 2 km away on the Cape Flattery cliffs.

Peregrines prey on species up to ca. 0.6 kg, which includes crows and Cassin's (*Ptychorampus aleuticus*) and Rhinoceros (*Cerorhinca monocerata*) auklets (Table 1). Above this mass, the falcon's effectiveness may be limited by size considerations: puffins (0.76 kg) and oystercatchers (0.68 kg) are conspicuous and available, but we never saw them under attack. Immature gulls (0.98 kg) and murre (1.01 kg) are only occasionally attacked successfully, although they are the most abundant apparent prey. Adult gulls (1.13 kg) and Pelagic Cormorants (*Phalacrocorax pelagicus*, 2.04 kg) were also conspicuously available and unattacked. Thus, if Peregrine Falcons influence the population biology of some of the heavier species, direct effects seem unlikely, and indirect processes must be invoked.

*Fork-tailed Storm-Petrel* (*Oceanodroma furcata*).—This species breeds on Tatoosh. The presumed evidence of falcon predation (feathers

TABLE 1. Direct observations of and corpse counts from Peregrine Falcon feeding. Prey ordered by increasing body mass (from Terres 1980, Reid 1987, unpubl. data). Asterisk indicates species known to breed on Tatoosh.

Species	Mass (kg)	Feeding observations	Eaten corpses
Savannah Sparrow ( <i>Passerculus sandwichensis</i> )	0.02	13	
Other passerines			4
Leach's Storm-Petrel ( <i>Oceanodroma leucorhoa</i> )*	0.04		6
Fork-tailed Storm-Petrel ( <i>O. furcata</i> )*	0.05		3
Cassin's Auklet ( <i>Ptychoramphus aleuticus</i> )*	0.17	4	43
Marbled Murrelet ( <i>Brachyramphus marmoratus</i> )	0.23		2
Green-winged Teal ( <i>Anas crecca</i> )	0.32		1
Black-legged Kittiwake ( <i>Rissa tridactyla</i> )	0.32		3
Northwestern Crow ( <i>Corvus caurinus</i> )*	0.42	3	8
Pigeon Guillemot ( <i>Cephus columba</i> )*	0.48		3
Heerman's Gull ( <i>Larus heermanni</i> )	0.54		1
Rhinoceros Auklet ( <i>Cerorhinca monocerata</i> )*	0.54	2	110
Black Oystercatcher ( <i>Haematopus bachmani</i> )*	0.68		
Tufted Puffin ( <i>Fratercula cirrhata</i> )*	0.76		
Glaucous-winged Gull (young) ( <i>L. glaucescens</i> )	0.98	1	7
Common Murre ( <i>Uria aalge</i> )*	1.01	2	6
Glaucous-winged Gull (adult) ( <i>L. glaucescens</i> )*	1.13		
Pelagic Cormorant ( <i>Phalacrocorax pelagicus</i> )*	2.04		
Brandt's Cormorant ( <i>P. penicillatus</i> )*	2.50		

and the presence of both wings) was found infrequently. Our best estimate of population trends is derived from mist-netting at a specific site. Netting was intense from 1978 to 1983 and has been maintained since with reduced effort. The minimal protocol was to set up a net shortly after dusk, and to record the time an individual was caught and the time the net was taken down. We estimated storm-petrel numbers as catch per unit effort, based on birds caught in a single 2.1-m  $\times$  12.8-m net (3.8-cm mesh), from the time the first individual was captured until the last individual was caught or 0130, whichever came first. We sampled in April, May, June, and early July.

There were no detectable trends in storm-petrels caught per hour (Fig. 2). Both population lows (1981 and 1984) are explicable. In 1981 a resident Western Screech-Owl (*Otus kennicottii*) fed on both species of storm-petrels. Presumably these activities reduced population numbers and disrupted nesting, at least in that year. The 1984 low is probably associated with a delayed effect of the 1982-1983 El Niño. Glaucous-winged Gulls (*Larus glaucescens*) on Tatoosh had minimal breeding success that year as well (Paine 1986). Fork-tailed Storm-Petrels showed no statistically significant trend through time, when years are treated as independent samples ( $P > 0.9$ ,  $r^2 = 0.214$ ). Neither was there a negative population response to the increasing falcon presence, probably because of the

petrels' nocturnal habits and maneuverability in flight.

*Leach's Storm-Petrel* (*Oceanodroma leucorhoa*).—Wahl et al. (1981) suggested that 300 birds breed on Tatoosh, although this estimate is probably low (ca. 1,500 individuals have been banded since 1978). Our population estimates are based on procedures identical to those employed for *O. furcata*. Again, no statistically significant temporal trends (Fig. 2) are present, although  $0.05 < P < 0.10$  when the poor 1984 breeding year is omitted (Spearman rank-correlation test). Although Leach's Storm-Petrels were occasionally eaten, no correlation exists between mist-net catch rates and falcon presence.

*Rhinoceros Auklet* (*Cerorhinca monocerata*).—These medium-sized alcids nested on Tatoosh,

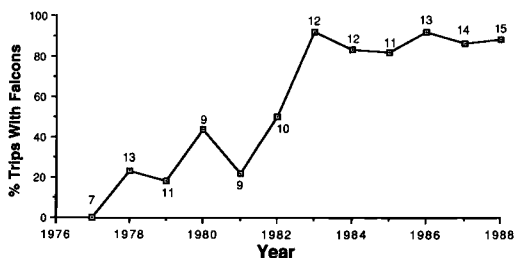


Fig. 1. Occurrence of Peregrine Falcons at Tatoosh as measured by the percentage of trips per year that falcons were observed. Numbers above points are the trips per year.

and their burrows riddled many of the salmonberry-covered slopes. We have no accurate population counts. Independent estimates range from 50 breeding birds (Manuwal and Campbell 1977), based on 1973–1974 census data, to 300 breeders (Wahl et al. 1981). Indirect evidence suggested an accumulated Peregrine Falcon impact.

We saw auklet corpses frequently. Those caught and consumed by Peregrine Falcons were characterized by the head remaining attached, and skin and feathers neatly pulled back. The neck, wing, breast and thigh musculature, and contents of the abdominal cavity were consumed. Some of the corpses were almost museum-quality preparations. Beak marks were sometimes visible around the rib cage. From 30 May to 29 August 1988, we counted all Rhinoceros Auklets killed by Peregrine Falcons, and we collected their corpses. In this 91-day interval, peregrines ate a minimum of 69 individuals. We do not know how many peregrines were involved, although it is unlikely to be more than two. These body counts represented a minimal mortality estimate. Some corpses were probably undiscovered because the island is large, has inaccessible areas, is heavily vegetated, and is partially washed by waves. Peregrines, however, tend to be creatures of habit and to feed at the same time and place daily, factors that improve the probability that kills would be discovered. Minimal mortality estimates are 0.76 birds per day during this interval. If there are 300 Rhinoceros Auklets on the island, the Peregrine Falcons consumed 23% of them in 1988 alone. Rhinoceros Auklets killed by peregrines have been found on Tatoosh since 1978, and they constitute the most abundant prey (Table 1).

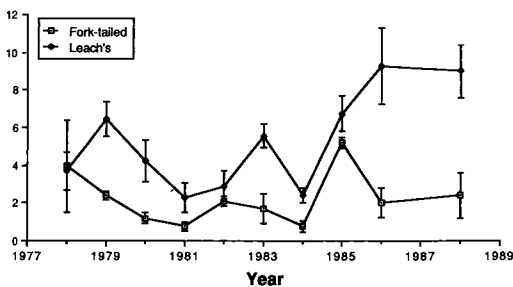


Fig. 2. The catch per hour of storm-petrels in a standardized mist net. There are no statistically significant trends in these data; vertical lines indicate  $\pm 1$  SE.

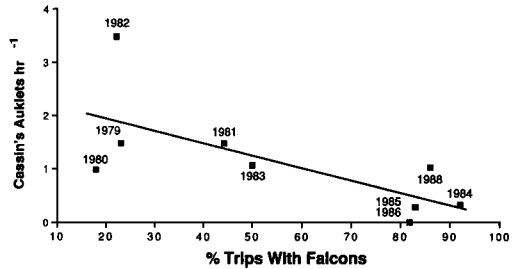


Fig. 3. Correlation between Cassin's Auklet and Peregrine Falcon presence in the previous year. Numbers indicate year of observation.

*Cassin's Auklet* (*Ptychoramphus aleuticus*).— These small alcids breed on Tatoosh. They are commonly heard calling in February and are often caught in mist nets from March to July. No reliable estimate of population size exists for Tatoosh, but Wahl et al. (1981) suggested 300 birds. Corpses, usually headless, are most common from February through June, and they probably mirror the period of peak availability to falcons. For instance, in June 1978 we collected 16 recent kills from the island's top. Between February and June 1988, we found 15 Cassin's Auklet corpses. Our estimates of Peregrine Falcon effects on population trends is based entirely on mist-net captures, which began in the first year (1979) in which March–July data were available. The mean number of Cassin's Auklets caught per hour was related inversely to the proportion of trips on which peregrines were sighted in the previous year (Fig. 3). This would be expected if a frequent prey species was being slowly decimated by an effective consumer (linear regression,  $r^2 = 0.73$ ,  $P < 0.01$ ). In addition, if the delayed El Niño effect of 1984 is omitted, a two-sample *t*-test suggests differences in the mean number of

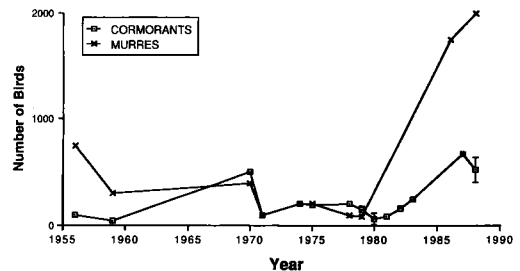


Fig. 4. Estimates of Pelagic Cormorant (open squares) and Common Murre (X) abundance at Tatoosh, 1956–1988. Vertical lines indicate  $\pm 1$  SE. Data before 1979 are from various sources.

auklets caught per night before (1979–1983) and after (1985, 1986, 1988) falcons became conspicuous ( $t = 2.07$ ,  $df = 35$ ,  $P < 0.05$ , one-tailed).

*Common Murre* (*Uria aalge*).—There is evidence of a dramatic increase in murre numbers during the last decade. First, population counts (1956–1979) suggest a Tatoosh breeding population of <1,000, and perhaps <500. More recently, we counted a minimum of 2,000 birds (Fig. 4). Second, casual observations suggest that the number of breeding sites has increased. From 1968 to the mid-1970s, murre nests were primarily on the cliffs. By 1980, numerous satellite colonies began to form. One of these was estimated to contain 39 pairs in 1981; in 1988, >300 birds were counted. Since the mid-1970s, small colonies have developed on the north, east, and south sides of Tatoosh. Although some of these contain as few as 10 pairs, at least one has between 700–1,000 birds. This site, on the southwest side of the island, occupies a 5–8-m-deep by 18-m-long band on the island's top, where the murre nests under salmonberry. Their activities have killed the salmonberry. This feature, readily recognizable in photographs, implies that this colony did not exist before 1980.

Falcons rarely prey on murre despite their abundance. Over the years, we found an occasional corpse that displayed the hallmarks of falcon predation. Murre are struck occasionally in the air by peregrines, although we could not determine whether the blows were fatal. Murre populations have not been influenced adversely by falcons. Conversely, the murre increase on Tatoosh parallels that of the falcons, suggesting that other factors are involved.

*Pelagic Cormorant* (*Phalacrocorax pelagicus*).—These birds, common cave and cliff nesters on Tatoosh, have increased over the last 30 yr, with a statistically significant spurt since 1980 (Fig. 4). We have never observed cormorants eaten or even harassed by the falcons. Instead, their change in numbers correlates (Spearman test,  $P < 0.05$ ) positively with relative Peregrine Falcon abundance.

*Black Oystercatcher* (*Haematopus bachmani*).—During 1986–1988, the breeding population of oystercatchers on Tatoosh Island ranged from 8 to 10 pairs. Data on clutch size and fledging success (considered the time at which the young could fly) were collected for 37 nests over these 4 yr. We excluded nests that failed because of human activity (Coast Guard nest vandalism), a severe storm, egg infertility,

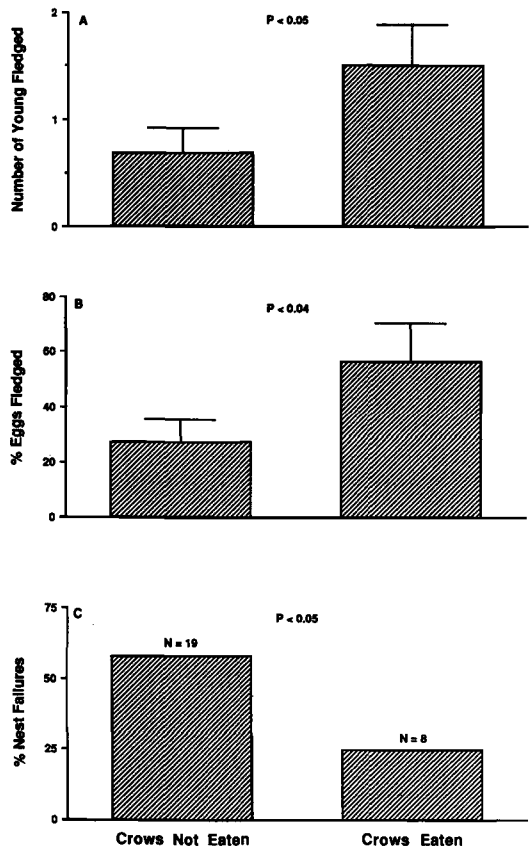


Fig. 5. The effects of crows on various indices of Black Oystercatcher reproductive success. Comparisons are between years in which crows were not eaten (1985, 1986, 1988) and that in which they were eaten by Peregrine Falcons (1987). All differences are significant; see text for details. Bars indicate 1 SE.

and one nest in which final outcome data were unavailable; a total of 27 nests remained.

We compared nesting success between the year (1987) when Peregrine Falcons fed heavily on crows (see below) and the years (1985, 1986, and 1988) when we found no evidence of falcon predation on crows. We observed crows eating oystercatcher eggs in 1985 and 1986. Oystercatcher clutch size did not differ between years (Mann-Whitney  $U$ -test,  $P > 0.6$ ). The number of young/nest fledged increased significantly when falcons fed on crows ( $U$ -test,  $P < 0.05$ , Fig. 5A), as did the percentage of eggs that eventually fledged ( $U$ -test,  $P < 0.04$ , Fig. 5B). The percentage of nests that failed completely was significantly greater in years when Peregrine Falcons did not feed on crows (binomial test,  $P < 0.05$ , Fig. 5C). Although the sample size is

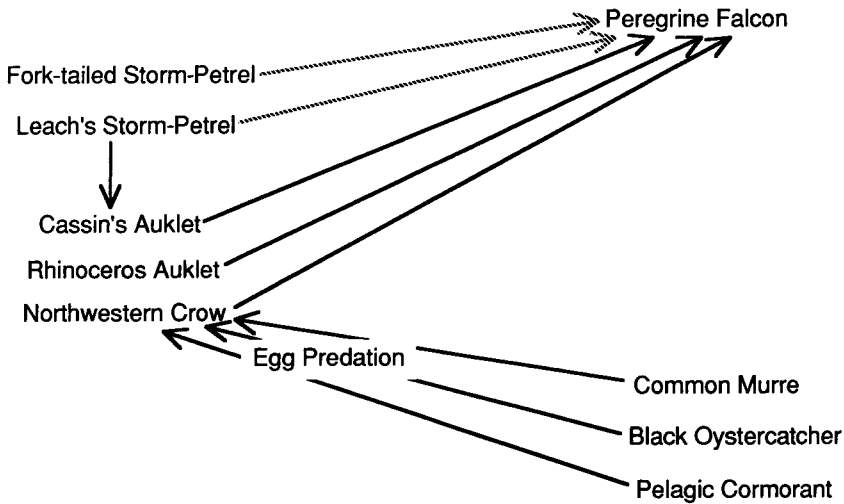


Fig. 6. Interaction pathways; falcon influence on seabirds at Tatoosh Island. Solid lines indicate major direct and indirect effects; dashed lines suggest less important participants.

small, the number of resident oystercatchers in 1985–1988 correlates positively with the percentage of trips with Peregrine Falcon observations ( $r^2 = 98.4\%$ ,  $P < 0.005$ ).

We believe the positive Peregrine Falcon influence on oystercatchers was mediated indirectly through the crow population. Conversely, we have never found dead oystercatchers that had the hallmarks of peregrine predation, despite our frequent observation of oystercatchers chasing falcons away from a chick.

*Northwestern Crow* (*Corvus caurinus*).—These birds are common breeders on Tatoosh. Population estimates are difficult because of the birds' gregarious nature and the continuing exchange of individuals with the mainland. Estimates made either before this study or independently are: 10+ birds, 1959 (F. R. Richardson); 20 birds, 1970 (D. R. Paulson); 15 birds, 1971 (M. Perrone); 10–15 birds, 1980 (G. B. Van Vliet). These numbers match our counts, which ranged from 8–30 birds during the spring and summer months.

Crow corpses were found occasionally. Until 1985, most were juveniles that had drowned, presumably on their initial flights out of nesting cavities in sea caves. Such drowned, uneaten individuals were not observed in 1986–1988, which implies a decline in crow nesting levels. We found a few adults eaten by falcons in 1979 and 1981. In April 1981, we observed a female Peregrine Falcon eating a crow. During that same summer on subsequent field trips, five fresh corpses were found in addition to another

direct observation at Tatoosh and one reported at Neah Bay.

Northwestern Crows, like other corvids, are effective egg and nest predators (Verbeek 1982, Shields and Parnell 1986). We often observed them stealing eggs from Pelagic Cormorant nests on Tatoosh. Their relationship to Glaucous-winged Gulls seems more enigmatic, and because we conscientiously tried to avoid disturbing nesting murres, we lack direct crow  $\times$  murre observations. One indicator of nest-raiding opportunity is the number of eggs destroyed by crows. We have used two measures. First, we routinely walk 500 m of grassy paths on the island's top. These are favored feeding places for crows. In 1988 we found the remains of 15 cormorant eggs and one gull egg. In 1987 eggs were absent from these paths. In earlier years, we found an estimated 30–80 eggs per breeding season. Second, the new murre colony at the island's southwestern tip was heavily preyed upon in 1984–1986, and murre eggs with penetrating beak marks littered the rocks beneath the colony. In 1987 and 1988, despite numerous searches, we found no eggs. The most likely reasons for reduced egg predation are fewer resident crows and suppression of their nest-raiding activities in the presence of falcons.

## DISCUSSION

We believe Peregrine Falcon activities have led to substantial changes in the species-abun-

dance or performance patterns within the Tatoosh marine bird assemblage (Fig. 6). The most consistent prey items of the Cape Flattery Peregrine Falcons (two species of auklet) probably are declining. Pelagic Cormorants and murres have increased because of crow suppression (Fig. 4). Oystercatchers are more productive in the presence of peregrines (Fig. 5) and may also be increasing. The trends in storm-petrel population cannot be linked directly to Peregrine Falcon activities. Instead, Leach's Storm-Petrels may benefit from the indirect effect of a release from competition with auklets for nesting space. Although the evidence for competition is circumstantial, there was a negative correlation between Leach's Storm-Petrel abundance and hourly catch of Cassin's Auklets after we excluded 1984, when both species seemed to respond to the aftermath of the El Niño by greatly reduced breeding (linear regression,  $r^2 = 0.44$ ,  $P < 0.05$ ). No relationship was found between Cassin's Auklets and Fork-tailed Storm-Petrels. Whittam and Siegel-Causey (1981) also found a strong, negative interaction between the same species in Alaskan seabird colonies. The primary argument favoring a diffuse Peregrine Falcon influence is the uniting within a biologically reasonable, observable, and measurable framework a variety of divergent population trends. Strong tests of the implied relationships are probably impossible. Thus a peregrine removal experiment would be unpopular. Another critical link, the crows, could be manipulated, which would generate testable consequences.

Four species have been purposely omitted from our model (Fig. 6). Pigeon Guillemots (*Cephus columba*) are abundant, but they are rarely eaten by peregrines (three records). Tufted Puffins (*Fratercula cirrhata*), with 70–120 breeding pairs, seem to be ignored by the falcons. The gull colony is large (ca. 2,000 pairs), and Peregrine Falcons (birds of the year?) feed on young gulls. Adult gulls, however, are ignored and often ride thermals near a falcon. Finally, Black-legged Kittiwakes (*Rissa tridactyla*), common at Cape Flattery until 1982, are eaten by peregrines. Whether their disappearance was due to falcon activity or was associated with the 1982–1983 El Niño is not known, although they continue to occur regularly off the Grays Harbor jetty (D. R. Paulson pers. comm.), ca. 175 km to the south.

Peregrines probably exert these general influences on bird populations over a regional

scale. Cade et al. (1988) documented increased peregrine abundance along the West Coast of North America. For example, only one peregrine nested in Oregon in 1979 (Henny and Nelson 1981); 6 nests were located in 1987 and 10 in 1988. Similar increases have occurred in California. In Washington, peregrines were common along the coast in the early 1900s (Jewett et al. 1953). There is little question of their decline and subsequent recovery (Fig. 1; Anonymous 1987, 1988), although the populations have probably not attained—and perhaps can never attain—their original levels.

Two alternative but nonexclusive hypotheses might also account for the observed changes in seabird populations. First, factors independent of birds might generate the observed patterns. Tatoosh's geographical position and recent history have exposed its bird population to three different, potentially harmful influences: oil spills, human disturbance, and El Niño events. The Strait of Juan de Fuca is a major shipping lane for the ports of Port Angeles, Tacoma, Vancouver, and Seattle. Before 1981, oiled seabirds (especially murres) were common. Tightened regulations regarding ballast cleaning and off-loading fuels have made both oiled birds and tarballs (i.e. essentially congealed bunker C fuel) increasingly rare. The Tatoosh Coast Guard facility was automated in November 1976. Our observations suggest little human impact on the island's avifauna. The 1982–1983 El Niño occurred approximately at the midpoint of our study. Oceanographic influences probably did not extend into Washington waters until after the 1982 breeding season, but they were conspicuous until late 1983 (Wooster and Fluharty 1985). The only known effects on breeding bird populations on the Washington outer coast occurred in 1984 (Paine 1986). We anticipated that the negative effects would be shared by all species, especially murres and cormorants; but, these populations increased dramatically (Fig. 4). The conflicting patterns of species increases and decreases pose interpretative problems for any of the above factors as the main causal agent.

Second, the observed population trends could be mediated by gulls. Glaucous-winged Gulls and other large gulls consume petrels and small alcids (Trapp 1979), take eggs, and overlap extensively with murres, cormorants, and even oystercatchers in their demands for suitable nesting habitat (Ainley and Lewis 1974). Perhaps the strongest argument against this hy-

pothesis is that there is little convincing evidence that the gulls have increased substantially in the last three decades: estimates of 2,000+ birds in 1959 (F. R. Richardson), 3,000+ in 1974 (Manuwal and Campbell 1977), 3,000+ in 1975 (Varoujean 1979), and 2,000 birds in 1978 (Wahl et al. 1981) are not much less than Wootton's 1986-1988 average of 3,800, which was based on much greater familiarity with Tatoosh's terrain and more counting time. Even if the gulls have increased modestly, cormorant numbers have approximately tripled since 1970, and murrens have increased by a factor of 4-5. A possible explanation is that gulls somehow inhibited the activities of crows. We have never observed this. The gull-crow relationship seems entirely asymmetric, with all advantages to the crows. The observed acts of predation and body counts (Rhinoceros Auklets) cannot be attributed to gulls. Similarly the great majority of the gulls nest on unvegetated or minimally vegetated rocky areas. Gulls therefore do not overlap spatially with breeding Cassin's Auklets and cannot be easily linked with their significant decline.

There are two final points to make. First, these seabird populations appear to be linked by a common predator rather than by competition for a varied resource. Approximately half of the effects are indirect, positive, and mediated by crow activity. They are not of the directly negative sort usually associated with consumer-victim dynamics. Second, the increasingly effective conservation effort to reestablish Peregrine Falcons is not without side effects, which should be considered in much greater detail. Near-shore, mixed-species nesting assemblages will assuredly be stressed by humans. Logging or other forms of habitat alteration, competition with fishermen, increased small boat traffic, or sundry forms of oceanic pollution due to oil or floating plastics are increasingly characteristic of the northeastern Pacific coastline. In the long run, continually increasing Peregrine Falcons, a species that adjusts well to human activities and structures, will surely add a complicating and emotionally charged factor to the total conservation picture.

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